Thermoregulation, Flight, and the Evolution of Wing Pattern in Pierid Butterflies: The Topography of Adaptive Landscapes

JOEL G. KINGSOLVER
Department of Zoology, NJ-15, University of Washington, Seattle, Washington 98195

SYNOPSIS. This paper describes a case study of adaptation, constraint, and evolutionary innovation in pierid butterflies. I develop a framework for discussing these issues that focuses on the questions: What is the form of the adaptive landscape relating fitness to phenotypic characters? How do such landscapes differ for evolutionarily related groups? I examine the evolution of wing pigment patterns and thermoregulatory behavior for butterflies in two subfamilies in the family Pieridae, with three principal results. First, I show that thermoregulation can be an important component of fitness in pierids, and that wing color and thermoregulatory behavior are important phenotypic characters determining thermoregulatory performance and the adaptive landscape. Second, I show how limits on possible variation in wing color and behavior constrain evolution within one subfamily of pierids, and how these constraints are set by the physical and biochemical mechanisms of adaptation. Third, I show how evolutionary innovation may have resulted from the addition of a new, behavioral dimension to the landscape, and how this addition has altered the functional interrelations among various elements of the wing color pattern. I suggest that comparative analyses of the form and determinants of the adaptive landscape may be useful in identifying evolutionary innovations, and complement theoretical analyses of evolutionary dynamics on such fitness surfaces.

INTRODUCTION

Adaptation and constraint

This paper presents a case study of adaptation, constraint, and evolutionary innovation in pierid butterflies. I begin by developing a framework for examining this case study that focuses attention on a more general issue: The topography of adaptive landscapes.

The adaptive landscape has been useful in studying adaptation and constraint both as a metaphor and as an analytic tool. In Wright’s (1931, 1969, 1977) original formulation, as part of his shifting balance theory of evolution, the adaptive landscape is the relation of mean population fitness to population gene frequencies; evolution is then represented as a trajectory on this fitness surface in gene frequency space. In recent quantitative genetic models of evolution (e.g., Lande, 1979; Lande and Arnold, 1983) the landscape is a fitness surface as functions of phenotypic character values.

The utility of the landscape concept lies in its representation of adaptation and evolutionary change. For natural selection without frequency dependence, evolution proceeds “uphill” (towards increasing mean population fitness) on the landscape surface for a variety of genetic systems (Fisher, 1930; Wright, 1931; Kingman, 1961; Lande, 1979); and evolutionary equilibria lie at or near peaks in the landscape. In this view, adaptation is the state of being on such adaptive peaks, or higher on the slope than some reference (e.g., ancestral, sister) group. In practice, most studies of adaptation relate genotypes or phenotypic characters to some measure of performance which is correlated to individual fitness, and adaptations are phenotypic characters that improve (or maximize) performance (Arnold, 1986).

Constraints on adaptive evolution are manifested as limits on genetic and phenotypic variation and covariation, and affect the population’s location and movement on the fitness surface. First, at any point in time the population occupies only a restricted region in phenotypic space, and thus experiences only a restricted region of the adaptive surface. (I assume here that the phenotypic space and its associated fit-
ness surface exist independent of the existence of populations currently occupying that space and surface: see Burger [1986] for discussion.) As a result, the ranges of genotypes and phenotypes in the population limit the available variation on which selection can act. Second, in quantitative genetic models phenotypic and genetic covariances strongly influence the rates and directions of evolution on the fitness surface (Lande, 1979, 1980; Lande and Arnold, 1985; Burger, 1986). Along these lines, several recent studies have modeled constraints by partitioning genetic variance-covariance into components attributed to developmental (Cheverud, 1984) and phylogenetic (Cheverud et al., 1985; see also Felsenstein, 1985) factors. At the same time, empirical studies have tried to demonstrate how developmental mechanisms determine the relation of genetic to phenotypic change, and to evaluate how such mechanisms may constrain phyletic change (Alberch et al., 1979; Alberch and Gale, 1985; Hanken, 1983). Thus, the adaptive landscape can provide a framework that represents both adaptation and constraint.

Topography of the landscape

Metaphorically, the discussion thus far might be considered the “statics and dynamics” of the adaptive landscape: Given a particular landscape, what factors determine evolutionary change along its surface? An alternative perspective, and the subject of this paper, might be called the “topography” of the landscape: What is the form of the landscape? What features of organisms and environments determine the form of this surface? To address these questions, we need first to decide what topographic features are of evolutionary importance, and second to locate such features in phenotypic (or gene frequency) space.

The analyses of evolutionary dynamics summarized above identify the important topographies: There are at least four general features that are relevant to the origin of evolutionary innovations. First, the rate of evolution is directly related to the selection gradient, or equivalently the steepness of the fitness surface (Fisher, 1930; Lande, 1979). Second, saddle points represent potential areas for disruptive selection and possible “branch” points between alternative adaptive peaks (Felsenstein, 1979; Kirkpatrick, 1982; Slatkin, 1984; Lande, 1985; Newman et al., 1985; Burger, 1986). Third, the addition of new dimensions to the landscape implies a range of phenotypic values for a character that was previously monomorphic (or absent). Fourth, ridges and inversions of curvature in the landscape represent regions where the nature of functional interrelationship between two or more characters is changing (Burger, 1986). Dobzhansky (1937) and others have mentioned the tendency of adaptive peaks to cluster close together, but the problem of locating important landscape features has not been systematically addressed. At least four general approaches come to mind: Survey, comparative, experimental, and a priori approaches. First, as suggested by Lande and Arnold (1983), one can use techniques from selection analysis to estimate the slope and curvature of the landscape (i.e., the selection gradient) for a series of populations and species. Such a survey would be extremely valuable in evaluating patterns of phenotypic selection in nature, but would yield primarily local estimates of the landscape at the current location of particular populations. Mitchell-Olds and Shaw (submitted) discuss some of the difficulties in statistical inference and biological interpretation with this approach. Second, a comparative approach among related taxa might be used to form a picture of the landscape from the fragments currently occupied by those taxa (see Felsenstein [1985] for a recent discussion of the comparative method and its methodological difficulties). Third, relevant experimental manipulation of phenotype can be used in some systems to systematically examine the relation of phenotype to fitness components. This approach may be particularly useful in evaluating the landscape surface in regions of phenotypic space not currently occupied by any populations. Fourth, one can try to identify a priori characteristics of organisms and/or environments that give rise to important topographic features: That is, to identify
evolutionary innovations. Clearly, these approaches are complementary, not mutually exclusive, but the a priori approach has not been systematically discussed, much less applied. The experimental approach has been frequently used to relate phenotype to fitness, but has not been systematically applied towards estimating the fitness surface in currently unoccupied phenotypic space.

A case study

In this paper I present a case study of adaptation, constraint, and evolutionary innovation from this perspective of the topography of the adaptive landscape, using primarily the comparative and experimental approaches. The study concerns the evolution of thermoregulation and wing color in pierid butterflies, and addresses the question: How do the adaptive landscapes relating wing color to thermoregulatory performance differ for evolutionarily related groups of pierids? There are three parts. First I show that thermoregulation can be an important component of fitness in pierids, and that wing color and thermoregulatory behavior are important phenotypic characters determining thermoregulatory performance and the adaptive landscape. Second, I show how limits on possible variation in wing color and behavior constrain evolution within one subfamily of pierids, and how these constraints are set by the physical and biochemical mechanisms of adaptation. Third, I show how evolutionary innovation in another pierid subfamily has resulted from the addition of a new, behavioral dimension to the adaptive landscape, and how this addition has altered the functional interrelations among other phenotypic characters. I suggest that such comparative analyses of adaptive topographies may be useful in identifying constraints and innovations in evolution.

Thermoregulation as a Component of Fitness

Most pierid butterflies require body temperatures of 28 to 40°C to take off and fly (Watt, 1968; Kingsolver, 1985a). They achieve these elevated body temperatures by behavioral thermoregulation, principally by orientation to solar radiation (review in Kingsolver, 1985b). The relationships between weather, body temperature, and flight activity have been quantified for Colias (Leigh and Smith, 1959; Watt, 1968; Roland, 1982; Kingsolver, 1983a, b), Pieris (Cappuccino and Kareiva, 1985; Kingsolver, 1985a; Ohsaki, 1986), and Anthocharis (Courtney and Duggan, 1983). One result that has emerged from these studies is that in many temperate populations of these species, weather strongly limits the amount of time available for flight activity. For example, in montane Colias species, the average available flight activity time ranged from 3 to 10 hr/day, depending on elevation (Kingsolver, 1983a); similar values have been reported for Pieris in montane Colorado (Kingsolver, unpublished results) and in Connecticut (Cappuccino and Kareiva, 1985), and Anthocharis in Great Britain (Courtney and Duggan, 1983). Many mark-recapture studies (reviewed in Courtney, 1986) have shown that the mean adult lifespan in most pierids is on the order of 3–7 days. These results suggest that available flight time may be a limited resource in many temperate pierid populations.

Because females must fly to find oviposition sites (and most pierids lay eggs singly on plants), one possible consequence of limitations on flight activity time is a reduction in realized fecundity of females. Three lines of evidence now support this hypothesis: 1) behavior, 2) demography, 3) and resource allocation.

1) Experiments in both field cages and environmental chambers with C. eurytheme, Anthocharis cardamines, and Pieris rapae show that daily egg production is correlated with air temperature and/or solar radiation (Stern and Smith, 1960; Gossard and Jones, 1977). For Colias in Colorado, Kingsolver (1983b) estimated realized fecundity by combining field data on available and realized flight times, activity budgets, longevity, and maximum oviposition rates; these estimates suggested that Colias in high elevation populations can lay only 20–50% of their full complement of eggs as a result of limited flight time.

2) Comprehensive population demographical studies have been done in three species of temperate...
pierids: *C. alexandra* (Hayes, 1981, 1984), *Anthocharis cardamines* (Courtney and Duggan, 1983), and *Leptidea sinapis* (Warren, 1981). In all three cases, the major determinant of population size is the realized fecundity of females in the previous generation. Courtney (1984) has recently summarized field data on realized fecundity in Lepidoptera, showing that the mean realized fecundity was less than ½ of the maximum for all species that lay eggs singly. In a general review of demographic studies of temperate Lepidoptera, Dempster (1983) showed that reductions in realized fecundity was the single most important factor determining population variation in 8 of 16 species studied.

3) Springer and Boggs (1986) examined oocyte production in two Colorado populations of *Colias philodice eriphyle* that differ significantly in their available flight activity times (Kingsolver, 1983a), to test the hypothesis that reduced flight time will select for reduced oocyte production. By rearing females from the two populations under identical conditions, they showed that the direction and magnitude of the difference between populations in number of oocytes are closely correlated with available flight activity time.

All of these results support the claim that “reduced fecundity as a consequence of poor weather seems to be a recurrent theme in pierid biology” (Courtney, 1986, p. 76).

Since the principal function of thermoregulation in pierids is to maintain the body temperatures needed for flight, this argues strongly that thermoregulation is an important component of fitness in temperate pierid butterflies, primarily via its effects on flight activity time. Thus we shall use flight activity time, subject to certain overheating constraints, as an indirect measure of fitness, and consider the relation of relevant phenotypic characters to the form of the flight time surface—i.e., the adaptive landscape.

**Thermoregulation and Wing Color in Sulfurs (Subfamily Coliadinae)**

**Thermoregulatory behavior and physical mechanisms**

Coliadine butterflies studied to date (*Colias* and *Nathalis*) use a specific thermoregulatory posture, lateral basking, to elevate their body temperatures into the range required for active flight (Watt, 1968; Douglas and Grula, 1978). In this posture (Fig. 1), the wings are closed over the dorsum, and the ventral hind wing (VHW) surface is oriented perpendicular to the solar beam; radiation is absorbed by the basal regions of the VHW, and the resulting heat is transferred to the body, elevating the body temperature. Because of the thinness and low thermal conductivity of the wings, only radiation absorbed in the basal portions of the VHW is effectively transferred as heat to the body. When the body temperature exceeds 40–42°C, *Colias* exhibits a heat-avoidance posture in which the wings and body are oriented parallel to the solar beam, reducing the radiative heat load. Thus, the ventral wing surfaces are used as radiation-absorbing devices.

One consequence of this behavior is that wing coloration affects radiation absorption and thus the body temperature of the butterfly. Wing coloration in *Colias* is determined by a two-pigment system: a black, melanic pigment and several yellow-orange pteridine pigments (Watt, 1967). The relative proportions of melanic- and pteridine-pigmented wing scales determine the wing color in a particular wing region. Because of the lateral basking posture and poorly conducting wings of *Colias*, only the wing color on the basal VHW is relevant to body temperature and thermoregulation; color in the other wing regions is thermally irrelevant (Kingsolver and Moffat, 1982). The aspect of wing color that is directly relevant to radiation absorption is the solar absorptivity, defined as the fraction of solar radiation striking a surface which is absorbed by it.

The degree of melanization on the basal VHW varies considerably biogeographically and seasonally in and among *Colias* species. Watt’s (1968, 1969) studies show that much of this variation is adaptive: greater melanization leads to higher body temperatures for a given set of environmental conditions, and heavy melanization is associated with populations in relatively colder conditions. Furthermore, VHW melanization is influenced by photoperiod (and in some cases, temperature) during...
Fig. 1. Common basking postures of butterflies. A) Definitions of the wing angle ($\theta$) and body orientation angle ($\gamma$) for a basking butterfly. B) Lateral, dorsal, and reflectance basking postures. Modified from Kingsolver (1985a).

Microevolution of wing color

If thermoregulatory performance, via its effects on available flight activity time, is a component of fitness, we may ask: What is the functional relationship of thermoregulatory characteristics like VHW color to fitness—that is, what is the form of the adaptive landscape? I have addressed this question by developing and testing a series of mechanistic models that relate weather conditions at a site and thermoregulatory characteristics of the butterfly to flight activity time (Kingsolver, 1983a; Kingsolver and Watt, 1983, 1984). Four characteristics of the butterfly are needed: body size (thoracic diameter); thermoregulatory posture; solar absorptivity of the basal VHW; and the thickness of “fur” (setae) on the ventral pterothorax. One important constraint in the model is that resulting from overheating: when butterflies experience body temperatures of 40-42°C, even when using the heat-avoidance posture, survivorship and fecundity are significantly reduced (Kingsolver and Watt, 1983). For present purposes, then, we can use such models to answer the following two questions: Given a set of meteorological conditions during the flight season at a particular site, and the thermoregulatory characteristics of a coliadine butterfly, what is the predicted mean daily available flight activity time? What is the probability that the butterfly will experience body temperatures in excess of 42°C, even if it uses the heat-avoidance posture?

Model simulations yield the predicted adaptive landscape, where wing absorptivity and thoracic fur thickness are the phenotypic characters and flight time (subject to the overheating constraint) is the component of fitness. Figure 2 gives landscapes for three sites where Colias butterflies have resident populations, along an elevational (and climatic) gradient in Colorado: Montrose, elevation h = 1.5 km, with a resident population of C. philodice eriphyle; Skyland, h = 2.8 km, with a separate population of C. p. eriphyle; and Mesa Seco, h = 3.3–3.6 km, with C. meadii. For each site, predicted flight time is given as a function of VHW absorptivity and fur thickness; those characteristics that violate an overheating constraint (where body temperatures exceeding 42°C occur more than 1% of the time) are also identified. Three points are worth mentioning. 1) For all sites, predicted flight time is a rapidly increasing function of VHW absorptivity, and this slope is particularly high for Mesa Seco, the highest elevation. If we consider flight time as a fitness component, this result implies that the selection gradient (sensu Lande and Arnold, 1983) is rather steep. 2) For each site, there is a combination of absorptivity and fur that yields the maximum flight time without violating the overheating constraint (defined as the optimum). The measured characteristics for the resident Colias population at each (given on the figures) yields a flight time quite similar to that for the optimum characteristics, especially for the higher elevation sites where flight time is limited. 3) Even when we consider the optimal phenotype for each site, there are large differences among the sites in available flight time (which are not due to differences in cloudiness among sites, since the meteorological data are for sunny days). In fact, the principal determinant of these differences is significant differences in short-term meteorological variation that affect the probability of overheating (see Kingsolver and Watt [1983, 1984] for detailed discussions). If the location of the ‘optimal’ phenotype in each environment is considered an adaptive peak, it is clear that the heights of these peaks for Colias are different in different environments.

Because changes in ventral wing melanism are the primary determinant of solar absorptivity in coliadines, it is useful to consider the landscape in terms of basal and medial/distal melanin (Fig. 6, top). This emphasizes two important results: That for any particular thermal environment there is an intermediate degree of basal mela-
Behavioral Innovation in Pierids

Constraints enter the landscape in two ways that underscore the utility of a model reflecting the mechanisms of adaptation. The two features that characterize thermoregulation in coliadines are the pteridine/melanin pigment systems for wing color determination, and the use of lateral basking as a thermoregulatory mechanism. The pigment systems define the range of possible wing absorptivities to between yellow (solar absorptivity $a = 0.4$) and black ($a = 0.7$); similarly the range of possible fur thicknesses that have useful thermal effects is from zero to about the size of the thoracic radius (Kingsolver and Moffat 1982; Kingsolver, 1983a). These ranges, which reflect the levels of variation in these characters for the genus Colias, explicitly define the parameter sets considered in the model. In fact, one can use these limits to identify the range of meteorological conditions to which “Colias-type” butterflies can adapt (Fig. 3). The second constraint, implicit in our model but equally important, is thermoregulatory posture. All coliadine butterflies studied to date use lateral basking, and this feature is one of the principal determinants of the functional relationship between VHW color and flight time. One can imagine other thermoregulatory mechanisms, not found in coliadines, that would change the form of the adaptive landscape.

I draw two conclusions from this analysis. First, Colias butterflies are indeed adapted for effective thermoregulation to the particular environmental conditions they experience, but because of constraints due to overheating the adaptive peaks differ in height in different thermal environments. Thus, the degree of local adaptation that can be attained by “Colias-type” butterflies may be limited in some selective

Fig. 2. Predicted flight time (hr./day) as a function of wing solar absorptivity (%) and thoracic fur thickness (mm) for Colias butterflies at three sites in central Colorado. Light lines plot values for different fur thicknesses from 0 to 1.5 mm as indicated. Heavy lines mark boundaries beyond which the overheating constraint, i.e., body temperature exceeds $42^\circ$C more than 1% of the time for a butterfly in heat-avoidance posture, is violated. Solid symbols with error bars are the predicted means, and standard deviations, of cumulative flight time based on observed means and standard deviations of absorptivity and fur thickness for resident male Colias at each site. (A) C. medius at Mesa Seco (■, 3.3-3.6 km elevation, (B) C. philodice eriphyle at Montrose (○, 1.5 km elevation), and C. p. eriphyle at Skyland (▲, 2.6-2.7 km elevation). See Kingsolver (1983a). The optimal solution (O) at each site is indicated. Modified from Kingsolver (1983a).
Fig. 3. Flight space diagrams, based on model simulations, indicating the ranges of wind speeds (cm/sec) and air temperatures (°C) in which Colias butterflies are able to achieve the body temperatures necessary for active flight. The area enclosed by the line is the flight space. For this plot, solar radiation load perpendicular to the solar beam is 110 mW/cm². Given are the flight spaces for two hypothetical Colias species, representing the extremes possible for "Colias-type" butterflies: C. maximus (solid line), with all-black wing bases and a thick fur layer; and C. minimus (dashed line), with all-yellow wing bases and no thoracic fur. See text. Modified from Kingsolver and Watt (1984).

environments. Second, the use of lateral basking posture as a thermoregulatory mechanism in coliadines determines the relationship of wing color to fitness; but the lack of variation in basking posture is a potential constraint on adaptive evolution in coliadines.

THERMOREGULATION AND WING COLOR IN WHITES (SUBFAMILY PIERINAE)

Thermoregulatory behavior and physical mechanisms

Pierines (subfamily Pierinae), like coliadines, use behavioral orientation to the sun for behavioral thermoregulation, and wing color plays an important thermoregulatory role. As in the coliadines Colias and Nathalis, the degree and pattern of wing melanization in the pierines Pieris, Tatophila, Phulia, Infraphulia, and Piercolias varies biogeographically both within and between species. In addition, melanization varies seasonally in some pierine species and is influenced by photoperiod during the larval period (reviews in Shapiro, 1976, 1984). There are, however, two important differences between pierines and coliadines relevant to thermoregulation. First, the background color for pierines is white on the dorsal wing surfaces, and white or yellow (occasionally orange) on the ventral surfaces. The yellow pigment in pierines is sepiapterin, one of the pterines found in coliadines, whereas the white pigment is primarily leucopterin (Watt, 1967). The concentration of sepiapterin in Pieris is controlled by a single locus with multiple alleles (Watt and Bowden, 1966), and individuals with yellow on the dorsal surfaces occur in many populations in pierines. Second, nearly all pierines studied to date (Infraphulia is a possible exception; Shapiro, 1985) use a thermoregulatory posture, apparently unique to the group, called reflectance basking (Fig. 1). As the name implies, in reflectance basking the wings are used as solar reflectors (Kingsolver,
The wings are held open at an angle, with the dorsal surface of the body oriented towards the solar beam; radiation is reflected off the white dorsal wing surfaces onto the body, increasing body temperature. On the other hand, at high body temperatures pierines use a heat-avoidance posture identical to that found in coliadines.

Microevolution of wing color in pierines

Mathematical and physical models, comparative studies, and experimental manipulations of wing pattern (Kingsolver, 1985a, b, 1987) reveal several interesting interactions between details of the basking posture (particularly the wing angle, or how far open the wings are) and the dorsal pattern of melanization (Fig. 4). First, the relationship of basking angle to body temperature depends on wing melanization pattern: the greater the amount of melanization on the wing margins, the larger the wing angle at which body temperature is maximized. Thus, for example, butterflies in the subgenera *Artogeia* and *Pontia*, which differ in the degree of marginal melanization, use significantly different basking wing angles. Furthermore, experimentally increasing the amount of black pigmentation on the dorsal margins in *Artogeia* produces a significant increase in the wing angle used during basking.

Second, the effect of melanization on body temperature depends on the wing region in question (Fig. 4). At the bases of the dorsal fore wings (DFW) and the anal regions of the dorsal hind wings (DHW) radiation absorbed by the wings can be effectively transferred as heat to the body; as a result, increased basal melanization increases body temperature. In contrast, increased melanization on the medial and distal wing surfaces decreases the high solar reflectivity (about 0.8 for white wing surfaces) that is needed for effective reflection of radiation to the body; as a result, increased melanization in these wing regions decreases body temperature. In fact, we can show that these different effects of melanization translate into effects on flight activity. For example, experimental manipulations with *Artogeia napi macdunoughii*, which has very little dorsal melanization, show that increasing basal black pigment leads to significantly earlier initiation of flight in the morning, whereas increasing marginal black pigment has the opposite effect on flight initiation (Kingsolver, 1987).

The thermal consequences of wing melanization can be summarized using a "functional map," which describes how melanization in specific wing regions affects body temperature (Fig. 5) (Kingsolver, 1987). Three general points emerge from a comparison of such maps for coliadines and pierines. First, for coliadines increased melanization either increases or has no effect on body temperature; for pierines, increased melanization can increase, decrease, or not affect body temperature depending on the wing region. Thus the function of wing melanization is partially reversed in the two groups. Second, the thermal effects and thermoregulatory function of melanization on the medial and distal dorsal wing surfaces in pierines depend critically on details of the ther-
moreregulatory posture, in particular wing angle, and one cannot interpret the functional significance of wing pattern without knowledge of such behaviors. Third, the difference in thermoregulatory mechanism between coliadines and pierines means that wing color in only a small portion of the wings affects thermoregulation in coliadines, while the entire dorsal wing surfaces may have thermoregulatory effects in pierines.

We do not yet have a model like that for Colias that relates quantitatively thermoregulatory behavior and wing color to body temperature and flight time, but we can construct some important qualitative features of the adaptive landscape surface for pierines (Fig. 6, bottom). First, reflectance basking represents a new dimension: It is a qualitatively different posture than lateral basking, and, unlike in laterally basking coliadines, there is a range of reflectance postures (in terms of wing angle) found in pierines. Second, one can no longer usefully speak of "wing melanization": Both basal and medial/distal wing regions can affect thermoregulatory performance in pierines (Fig. 6, bottom), in contrast to coliadines (Fig. 6, top). Furthermore, the functional interrelationships for melanization in different wing regions changes qualitatively as one moves from lateral to reflectance basking, and as reflectance wing angle changes, generating an inversion of curvature in the adap-
Behavioral Innovation in Pierids

There are two differences relevant to thermoregulation between coliadine and pierine butterflies: Background pigment and basking posture. The genetic basis for the difference in pigmentation is rather simple. The usual white background in pierines results from the pteridine pigment leucopterin, but a yellow background due to the pteridine sepiapterin occurs in many pierines, and is controlled by a single locus, multiple allele system. The yellow and orange background in coliadines results from several pteridines, including sepiapterin; but a white background, again due to leucopterin, is found in the “alba” form of females of many coliadine species, and is controlled by a single gene locus (Watt, 1973). Thus, the transition from yellow to white and its converse has a simple genetic basis in both groups. The second difference is in basking posture—the position of the wings and body relative to the sun. The genetic basis for this behavioral difference is unknown, but in pierines our experiments show that it is actually quite plastic for an individual butterfly.

The result of these two differences is that the functional significance and nature of selection on wing melanization pattern is qualitatively different in these two groups: For some wing regions the direction of potential selection is actually reversed. Clearly behavioral posture is an important element in understanding wing color evolution in this butterfly family. In terms of the adaptive landscape for pierids, the changes in background color and basking posture have two effects: the addition of a new behavioral dimension, and an inversion of curvature of the fitness surface with respect to melanization—two key topographic features for evolutionary innovation (see Introduction).

Cladistic analyses based on other morphological characters (Ackery, 1984) indicate that the Pierinae and the Coliadinae are each a monophyletic group. The sister group relations among these and the other two, less common, pierid subfamilies are still unclear. Thus far, the reflectance basking posture is only known among pierines in association with their characteristic white background, and likely is a derived character; lateral basking is apparently the rule in the other pierid subfamilies.

To understand the evolution of thermoregulation in pierines, then, one must account for both the novel posture and the characteristic background pigment of the group. But which came first, the pigment or the posture? I would argue that the pigment is the more likely first step, on three grounds. First, both white and yellow backgrounds are found in the pierines and in the coliadines, with a simple genetic basis, which suggests a common ancestry. Second, there is no known variation in basking posture in coliadines: all species studied to date use lateral basking. In contrast, there is considerable variation in posture in pierines, both within and among species. Not only are there differences in wing angle used during reflectance basking, but several species apparently use dorsal basking (Shapiro, 1985; Kingsolver, unpublished). Most importantly, female Pieris sometimes also use lateral basking, generally when they are not flying frequently (Kingsolver, unpublished; Wiernasz, unpublished); and male and female Tatochila and Infraphulia sometimes use lateral basking during initial warm-up after emerging from roosting sites (D. Wiernasz, personal communication). Thus, reflectance basking may not be the only posture used among pierines. Third, the posture is functionally useless for thermoregulation without white wings, but the converse is not true. “Alba” (white) Colias females are just as effective in thermoregulating using lateral basking as wild-type females (Watt, 1973). The reason is that in cold environments it is the amount of melanized wing scales on the VHW that is important; here the difference between white vs. yellow scales is trivial. In very warm environments where overheating is a potential problem, white could in fact be superior to yellow for thermoregulation. A glance at the flight spaces for Colias clarifies these points (Fig. 3). In contrast, mathematical and physical models show that
reflectance basking with yellow wings would only be 25% as effective in increasing body temperature as with white wings (Kingsolver, 1985a). Thus, it is unlikely that this thermoregulatory posture would have been established in pierines (or their ancestors) before the white pigmentation.

Note that white pigmentation need not have evolved as an adaptation for thermoregulation, because white pigmentation may have served other functions in pierines and their immediate ancestors. For example, several studies show that some *Pieris* species are relatively unpalatable to bird predators, resulting from sequestering of compounds from their cruciferous host plants (Jones, 1932; Marsh and Rothschild, 1974; Kingsolver, in preparation), and it has been suggested that white represents a type of aposematic coloration in pierines (Rothschild, 1981). In *Colias*, and presumably in *Pieris*, the white-yellow polymorphism in females affects the nitrogen balance such that white females mature more oocytes than yellow females (Watt, 1973). Which if any of these was the original function of white pigmentation is unknown.

If this scenario is correct, the change in posture from lateral to reflectance basking represents a major event in the evolution of wing patterns in pierids. We are uncustomed to thinking that such “small” behavioral changes could represent important evolutionary change, particularly at the subfamily level; behavioral characters are often considered relatively (compared to morphological characters) plastic phenotypic characters. This points to one of the general lessons of this study: There is no simple relationship between the degree of change in a phenotypic character and its effects on functional performance, on which selection can act. In terms of the adaptive landscape, this simply means that the fitness surface may be steep and/or bumpy in particular directions and particular locations.

I have presented this study of pierid evolution to show how, using a combination of experiments, observations, and models with a comparative analysis, one might try to analyse the topography of an adaptive landscape, and to use those analyses to locate topographic features associated with evolutionary innovations. What cues might one use to identify such features a priori? The present study might provide one possible cue: It is the change in physical mechanism, from radiation absorption to radiation reflectance, that drives the important features of the pierid landscape. In his studies of Actinopterygian fish, Lauder (1982) suggested that the existence of two different biomechanical pathways for jaw opening enabled the structural and functional diversification of this group. Whether these or other cues can be used to locate important topographic features remains to be seen.

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